Main prey and predators of northern shrimp (*Pandalus borealis*) in the northern Gulf of St. Lawrence during the mid-1980s, mid-1990s, and early 2000s

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2006

Canadian Technical Report of
Fisheries and Aquatic Sciences 2639

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Fisheries and Aquatic Sciences

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Cat. No. Fs 97–6/2639E ISSN 0706–6457

Correct citation for this publication:

Savenkoff, C., L. Savard, B. Morin, and D. Chabot. 2006. Main prey and predators of northern shrimp (*Pandalus borealis*) in the northern Gulf of St. Lawrence during the mid-1980s, mid-1990s, and early 2000s. Can. Tech. Rep. Fish. Aquat. Sci. 2639: v+28 pp.

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ABSTRACT

Savenkoff, C., L. Savard, B. Morin, and D. Chabot. 2006. Main prey and predators of northern shrimp (*Pandalus borealis*) in the northern Gulf of St. Lawrence during the mid-1980s, mid-1990s, and early 2000s. Can. Tech. Rep. Fish. Aquat. Sci. 2639: v+28 pp.

We used results of mass-balance models to describe the changes in the structure and functioning of the northern Gulf of St. Lawrence ecosystem related to northern shrimp (*Pandalus borealis*) for the mid-1980s, the mid-1990s, and the early 2000s. The net decrease in biomass of the large-bodied demersal species and the ensuing drop in predation in the mid-1990s may explain the increase in abundance of the northern shrimp at the end of the 1990s. Shrimp was among the main prey species, and predation was the main cause of shrimp mortality for all time periods. Greenland halibut (*Reinhardtius hippoglossoides*) progressively replaced cod (*Gadus morhua*) and redfish (*Sebastes* spp.) as the main shrimp predators. Since the biomass of Greenland halibut sharply increased since 1995, its effect via predation as well as fishing pressure should be considered in the elaboration of management strategies for shrimp in the northern Gulf of St. Lawrence.

RÉSUMÉ

Savenkoff, C., L. Savard, B. Morin, and D. Chabot. 2006. Main prey and predators of northern shrimp (*Pandalus borealis*) in the northern Gulf of St. Lawrence during the mid-1980s, mid-1990s, and early 2000s. Can. Tech. Rep. Fish. Aquat. Sci. 2639: v+28 pp.

Nous avons utilisé les résultats de modèles d'équilibre de masse pour décrire les changements dans la structure et le fonctionnement de l'écosystème du nord du golfe du Saint-Laurent associés à la crevette nordique (*Pandalus borealis*) pour le milieu des années 1980, le milieu des années 1990 et le début des années 2000. La forte diminution des biomasses des grandes espèces démersales et la chute résultante de leur prédation au milieu des années 1990 pourraient expliquer l'augmentation de l'abondance de la crevette nordique à la fin des années 1990. La crevette était parmi les principales proies et la prédation était la principale cause de mortalité de la crevette à chaque période de temps. Le flétan du Groenland (*Reinhardtius hippoglossoides*) a remplacé progressivement la morue (*Gadus morhua*) et le sébaste (*Sebastes* spp.) comme principal prédateur de la crevette. Étant donné que la biomasse du flétan du Groenland a augmenté grandement depuis 1995, l'effet de la prédation, en plus de la pêche, devraient être considérés dans l'élaboration des stratégies de gestion pour la crevette du nord du golfe du St. Laurent.

106-04097/

INTRODUCTION

In the northern Gulf of St. Lawrence (Figure 1), the ecosystem structure shifted dramatically from one previously dominated by piscivorous demersal fish (cod [*Gadus morhua*], redfish [*Sebastes* spp.]) and small-bodied forage species (e.g., capelin [*Mallotus villosus*], mackerel [*Scomber scombrus*], herring [*Clupea harengus*], shrimp [mostly northern shrimp, *Pandalus borealis*]) to a structure now dominated by small-bodied forage species and marine mammals (Savenkoff et al. 2004a and submitted[1]). Overfishing removed a functional group, large piscivorous fish, which has not recovered ten years after the cessation of heavy fishing. This has left only marine mammals such as seals and cetaceans as top predators during the mid-1990s, although small Greenland halibut (*Reinhardtius hippoglossoides*) became important predators in the northern Gulf during the early 2000s. These changes were accompanied by a decrease in total commercial landings and a transition in harvesting from long-lived and piscivorous groundfish toward planktivorous pelagic fish and invertebrates (Figure 2). This trend is unfortunately widespread in fisheries throughout the northern hemisphere and is indicative of overfishing (Pauly et al. 1998).

The changes that occurred in the northern Gulf of St. Lawrence over the past 20 years were driven by human exploitation of selected species and would largely qualify as a fishery-induced regime shift (Savenkoff et al. submitted[1]). Such shifts from ecosystems dominated by demersal fish to ecosystems dominated by pelagic fish and crustaceans have been documented in the Atlantic and the Baltic (Worm and Myers 2003, Frank et al. 2005) and other coastal ecosystems (Jackson et al. 2001). Large piscivorous predators declined dramatically, but their prey (herring, capelin, shrimp, and snow crab) increased in landings and abundance (Lilly 1991, Berenboim et al. 2000, Garrison and Link 2000, Koeller 2000, Lilly et al. 2000). In the northern Gulf, only capelin and shrimp among forage species showed an increase in biomass following the net decrease in biomass of large piscivorous predators (Savenkoff et al. submitted[1]).

Northern shrimp sustains an important trawl fishery in the northern Gulf (Savard et al. 2003). The fishery began in 1965 and catches increased progressively to reach about 26,000 tons in 2000, with a landed value of $40 million. The status of these stocks is determined annually by examining a number of indicators from the commercial fishery and research surveys (Savard and Bouchard 2004). In response to increases in abundance indices in the second half of the 1990s, total allowable catches (TACs) were raised by more than 70% between 1995 and 2001. Based on the results of mass-balance models, we present in this report the changes in the structure and functioning of the northern Gulf ecosystem for the mid-1980s, the mid-1990s, and the early 2000s as they relate to the shrimp stocks. Our results enabled us to evaluate the main prey and predators of shrimp as well as the effects of fishing and predation on this species for each time period.

[1]: Savenkoff, C., Castonguay, M., Chabot, D., Bourdages, H., Morissette, L., and Hammill, M. O. Changes in the northern Gulf of St. Lawrence ecosystem estimated by inverse modelling: Evidence of a fishery-induced regime shift? Submitted for publication.

MATERIAL AND METHODS

Data used in modelling

The data set covers a region of the northern Gulf of St. Lawrence (NAFO division 4RS, depth ≥ 37 m) equivalent to a total area of 103,812 km^2 (Figure 1). Infra-littoral species and American lobster (*Homarus americanus*) were not included in this study because exchanges between infra-littoral and pelagic zones are poorly understood and because the nearshore region (depths < 37 m) was not sampled by the annual summer bottom-trawl surveys. The sampling area used in our models for the calculation of densities represents the surface of strata sampled for the summer research survey in the northern Gulf of St. Lawrence (Bourdages et al. 2003).

The periods covered by this analysis are the mid-1980s (1985-1987), before the collapse of groundfish stocks in most areas of the Northwest Atlantic; the mid-1990s (1994-1996), after the collapse of groundfish stocks; and the early 2000s (2000-2002), at the end of the moratorium on cod fishing corresponding to a period of high abundance of shrimp and Greenland halibut.

Based on data availability and the ecological and commercial significance of the species, the organisms inhabiting the northern Gulf of St. Lawrence were divided into different functional groups or compartments (32 for the mid-1980s and mid-1990s, 31 for the early 2000s) (Table 1). The model structure for the early 2000s differs slightly from that used for the mid-1980s and mid-1990s for the following reasons: (1) improved refinements: cetaceans were separated into mysticeti (baleen whales) and odontoceti (toothed whales); (2) newly available data on biomass of size classes for shrimp and crabs that allowed separating these species into small and large groups for the early 2000s; (3) very low species biomass for the early 2000s: sand lance *Ammodytes* spp. were included in the planktivorous small pelagic feeders group for the early 2000s (biomass: 0.003 t km^{-2} vs 2.398 and 0.120 t km^{-2} for the mid-1980s and mid-1990s, respectively); (4) a combination of limited data and a weak trophic role in the mid-1980s and mid-1990s ecosystems for hooded seals (*Cystophora cristata*), harbour seals (*Phoca vitulina*), and Arctic cod (*Boreogadus saida*) resulted in these groups being combined with the harp seal (*Pagophilus groenlandicus*), grey seal (*Halichoerus grypus*), and capelin (*Mallotus villosus*) groups, respectively for the early 2000s.

For the mid-1980s and mid-1990s, we distinguished five marine mammal groups, one seabird group, sixteen fish groups, eight invertebrate groups, one phytoplankton group, and one detritus group (Morissette et al. 2003; Savenkoff et al. 2004a). For the early 2000s, we distinguished four marine mammal groups, one seabird group, fourteen fish groups, ten invertebrate groups, one phytoplankton group, and one detritus group (Savenkoff et al. 2005).

Some groups such as large pelagic feeders and large demersal feeders are composite groups, where the species were aggregated on the basis of similarity in size and ecological role. Cod, Greenland halibut, and for the early 2000s model, shrimp and crabs, were each separated into two groups based on diet, age/size at first capture, and age/size at maturity. Smaller fish prey mainly on invertebrates while larger fish feed mainly on fish. These changes tend to occur gradually with increasing length, but here it was assumed that the change occurs at 35 cm for cod (Lilly 1991) and 40 cm for Greenland halibut (Bowering and Lilly 1992). Based on an average size at sex change (22 mm carapace length, CL), shrimp were separated into large shrimp (≥ 22 mm CL), mainly female *Pandalus borealis*, which are recruited to the fishery, and small shrimp (< 22 mm CL), mainly juvenile and male *P. borealis* and individuals from other shrimp species, which are partially recruited to the fishery (Savard and Bouchard 2004). Based on large

differences in diet, vulnerability to predation (in particular cannibalism; crab prey ranged between 3.9 and 48.8 mm carapace width, CW), and minimal carapace width of adult snow crabs (40 mm CW), crabs were separated into small (≤ 45 mm CW) and large (> 45 mm CW) categories (Lovrich and Sainte-Marie 1997). Only large crabs are fished and consist almost exclusively of male snow crab, *Chionoecetes opilio*. Due to a lack of length-frequency data and information on diet compositions of small versus large fish as well as on the proportions of juvenile and adult fish in the diets of their predators, we could not distinguish juveniles and adults for other fish species.

To estimate the magnitude of trophic fluxes, the models require measurements or estimates of different parameters (input data) such as biomass, diet composition, and commercial fishery catches as well as consumption and production rates for different living compartments. In the inverse approach, we use local measurements (e.g., catches), information on the trophic structure of the ecosystem (e.g., diet composition), and measurements of specific processes (e.g., production and consumption) to reconstruct the interactions and to estimate flows (in t km^{-2} yr^{-1}) such as respiration, egestion, predation or other causes of mortality for each functional group. Diet composition and the other input data (biomass, production, consumption, and export) for each compartment as well as calculation details are described in Morissette et al. (2003) for the mid-1980s, Savenkoff et al. (2004a) for the mid-1990s, and Savenkoff et al. (2005) for the early 2000s. These technical reports are available online: www.osl.gc.ca/cdeena/en/publications.shtml.

Inverse modelling

Inverse models use mass-balance principles and an objective least-squares criterion to estimate flows of organic matter or energy among components of an ecosystem and to generate a "snapshot" of the system at one moment in time (Vézina and Platt 1988; Savenkoff et al. 2004b). As opposed to traditional approaches, the ecosystem is considered as a whole, taking into account trophic interactions between all functional groups. Inverse methods provide a powerful tool to estimate ecosystem flows using limited data, straightforward mass balance, and metabolic constraints.

In inverse modelling, we assumed that there was no change in biomass during each studied time period and that net migration was zero (migration out of or into the study area, food intake of predators that are not part of the system, etc.). Under this steady-state assumption, the sum of inflows (consumption for each consumer group) is balanced by the sum of outflows (production, respiration, and egestion for each consumer group). Also, production is equal to the biomass lost to fishing, predation, and natural mortality other than predation (hereafter termed other mortality causes). Other mortality causes could include other natural causes of death such as disease or could reflect unsuspected processes occurring in the ecosystem, such as misreported catches (e.g., Savenkoff et al. 2004b), unsuspected migration, or other processes not accounted for in the model. For phytoplankton, the net (corrected for respiration) production must balance the sum of the outputs (phytoplankton mortality including the egestion term and consumption of phytoplankton). For the detritus group, the inputs (egestion and other natural causes of death for other groups) must balance the sum of the outputs (consumption of detritus, bacterial remineralization of detritus, and burial). As bacteria were considered part of the detritus, detritus were assumed to respire. Details of the model structure and method of solution for the different equations are given in Savenkoff et al. (2004b and submitted).

The models are useful in constraining observations into coherent pictures (Savenkoff et al. 2004b and submitted); however, since the number of flows to be solved exceeds the number of independent mass balance relations (i.e., an underdetermined system), there is no unique solution to any model. Also, it remains that the results are sensitive to some choices we made regarding the modelling structure and that other valid solutions might be possible. However, for each model presented in the next section, the final solution is always the mean of 30 iterations with random perturbations of the input data (to a maximum of their standard deviations) and one solution without perturbation (the "initial solution") to provide an overall view of the ecosystem and to identify robust patterns. The estimated flows fell inside our *a priori* constraints and therefore were a reasonable "middle ground" description. Simulated inverse analyses have shown that the general flow structure of ecosystems can be recovered with these techniques, although the details can be inaccurate (Vézina and Pahlow 2003).

Background on shrimp

The key species, northern shrimp, dominates the biomass of the shrimp-like species in the northern Gulf and sustains the important commercial fishery. Generally, northern shrimp are found throughout the Estuary and the northern Gulf of St. Lawrence at depths of 150–350 m, but migrations do occur during breeding (females migrate to shallower waters in winter) and feeding (at night, shrimp leave the ocean floor to feed on small planktonic organisms) (DFO 2002). The striped shrimp, *Pandalus montagui*, is also found in the northern Gulf, but is much less abundant.

Input data (biomass, production, consumption, and commercial catch) used in modelling and estimated fluxes for shrimp for each time period are summarized in Table 2. Several scenarios were tested for 1985–1987. Here, we used the estimates from the most realistic solution, the "misreporting solution" that included misreported catches of large cod (Savenkoff et al. 2004a). In this solution, the catches of large cod have been increased by 30%, a level consistent with estimates of misreported cod catches in the northern Gulf in the mid-1980s (Savenkoff et al. 2004a). Some values were slightly different from data published in previous technical reports (Morissette et al. 2003, Savenkoff et al. 2004a, Savenkoff et al. 2005) due to model updates.

Catch

Data on commercial landings of northern shrimp are available since 1965 for the three management units in the northern Gulf: Sept-Îles, Anticosti, and Esquiman (Savard and Bouchard 2004). The mean annual total catch was 9,757 t or 0.09 t km^{-2} yr^{-1} (SD: 0.01 t km^{-2} yr^{-1}; range: 0.08-0.11 t km^{-2} yr^{-1}) during the mid-1980s and 15,913 t or 0.15 t km^{-2} yr^{-1} (SD: 0.01 t km^{-2} yr^{-1}; range: 0.14-0.17 t km^{-2} yr^{-1}) during the mid-1990s. In the early 2000s, shrimp were separated into large shrimp (≥ 22 mm CL) and small shrimp (< 22 mm CL). Female and male shrimp were not distinguished in commercial landings. Since length frequencies between commercial landings and annual summer bottom-trawl surveys are very similar, we used the sex-ratio established from the scientific surveys to separate the commercial catch into females and males in the early 2000s. The annual total landings from 2000 to 2002 were 14,832 t or 0.14 t km^{-2} yr^{-1} (SD: 0.02 t km^{-2} yr^{-1}; range: 0.12-0.16 t km^{-2} yr^{-1}) for females and 9,746 t or 0.09 t km^{-2} yr^{-1} (SD: 0.02 t km^{-2} yr^{-1};

range: 0.08-0.11 t km^{-2} yr^{-1}) for males. Modelling catch estimates were 0.09 t km^{-2} yr^{-1} for 1985–1987 and 0.16 t km^{-2} yr^{-1} for 1994–1996. For 2000–2002, the catch estimate was 0.15 and 0.09 t km^{-2} yr^{-1} for females and males, respectively.

Biomass

Shrimp biomass was calculated from summer research surveys covering NAFO divisions 4RS during each time period (Savard and Hurtubise 1991, Savard and Bouchard 2004). Mean biomass was 86,210 t or 0.83 t km^{-2} (SD: 0.56 t km^{-2}) during the mid-1980s, 63,872 t or 0.62 t km^{-2} (SD: 0.23 t km^{-2}) during the mid-1990s, and 98,240 t or 0.95 ± 0.21 t km^{-2} for females and 64,031 t or 0.62 ± 0.13 t km^{-2} for males during the early 2000s.

Production

Due to the lack of information on production (P) and total mortality (Z) for shrimp in NAFO divisions 4RS, it was assumed that production was equivalent to biomass multiplied by natural mortality (M), plus catch (Allen 1971). Natural mortality was assumed to be between 0.64 yr^{-1} (Fréchette and Labonté 1981) and 1.45 yr^{-1} (Bundy et al. 2000). When the minimum and maximum biomass values were used for each time period, we obtained production ranges of 0.37 to 1.57 t km^{-2} yr^{-1} (mean: 0.87 ± 0.51 t km^{-2} yr^{-1}) for 1985–1987 and 0.24 to 1.22 t km^{-2} yr^{-1} (mean: 0.64 ± 0.41 t km^{-2} yr^{-1}) for 1994–1996. For 2000–2002, the production ranges were 0.46 to 1.63 t km^{-2} yr^{-1} (mean: 0.96 ± 0.50 t km^{-2} yr^{-1}) for females and 0.30 to 1.04 t km^{-2} yr^{-1} (mean: 0.63 ± 0.32 t km^{-2} yr^{-1}) for males. The modelling production estimate for shrimp was 1.47 and 0.59 t km^{-2} yr^{-1} for 1985–1987 and 1994–1996, respectively. For 2000–2002, the production estimate was 1.04 and 0.89 t km^{-2} yr^{-1} for females and males, respectively.

Consumption

In the absence of information on food consumption by northern shrimp, consumption was only estimated by using the gross growth efficiency (GE, the ratio of production to consumption; 10–30%; Christensen and Pauly, 1992). Based on the mean production for each period and the minimum and maximum gross growth efficiency limits, we obtained consumption ranges of 2.89 to 8.68 t km^{-2} yr^{-1} for 1985–1987 and 2.13 to 6.40 t km^{-2} yr^{-1} for 1994–1996. For 2000–2002, the lower and upper consumption limits were 3.20 and 9.61 t km^{-2} yr^{-1} for females and 2.08 and 6.25 t km^{-2} yr^{-1} for males. The inverse solution estimated a consumption of 6.67 t km^{-2} yr^{-1} for 1985–1987 and 2.63 t km^{-2} yr^{-1} for 1994–1996. For 2000–2002, the consumption estimate was 5.97 and 4.50 t km^{-2} yr^{-1} for females and males, respectively.

Diet composition

For shrimp, feeding occurs in both the benthic and pelagic environments, in accordance with their diel vertical migrations. In their model, Bundy et al. (2000) assumed that 30% of the

total diet is benthic and 70% is pelagic. Annelids, small crustaceans, phytoplankton, and detritus were the main prey during the day while copepods and euphausiids were the principal prey items during the nocturnal migration. We used this diet composition for each time period (Tables 3 and 4).

RESULTS

Main prey groups consumed by shrimp

Shrimp mainly consumed detritus, small zooplankton, large zooplankton, and phytoplankton for each period (Figure 3). Large zooplankton are organisms and species greater than 5 mm in length and include euphausiids (mainly *Thysanoessa raschii, T. inermis*, and *Meganyctiphanes norvegica)*, chaetognaths (mainly *Sagitta elegans*), hyperiid amphipods (mainly *Themisto libellula, Parathemisto abyssorum*, and *P. gaudichaudii*), jellyfish (cnidarians and ctenophores), mysids (mainly *Boreomysis arctica*), tunicates, and ichthyoplankton. The small zooplankton includes zooplankton less than or equal to 5 mm in length. Copepods, mainly *Calanus finmarchicus, C. hyperboreus*, and *Oithona similis*, are the most numerous species of small zooplankton (Roy et al. 2000). In our inverse models, we were not able to estimate the individual proportion of each species aggregated in large and small zooplankton groups consumed by shrimp. During the early 2000s, the proportion of small zooplankton in the diet composition of shrimp increased (Figure 3). The diet compositions for females and males were very similar for the early 2000s (Figure 3 and Table 4).

These changes in the proportion of the different prey types ingested by shrimp should be interpreted with caution since we used the same diet composition to constrain the three models. Differences in the estimated proportions of prey consumed by shrimp were therefore related to mass conservation, trophic interactions among groups, and eco-physiological constraints specific to each time period modelled.

Role played by shrimp in the northern Gulf ecosystem

Shrimp was among the main prey groups in each time period (Figure 4). When planktonic and benthic invertebrate groups were not considered, capelin was the major prey in the system and accounted for 57% of all matter consumed within the ecosystem during the mid-1980s. The other main prey groups were planktivorous small pelagics (mainly herring, 15%), redfish (8%), and shrimp (7%) during the mid-1980s. There was a four-fold decrease in the matter consumed from the mid-1980s to mid-1990s (from 19.1 ± 3.0 to 4.8 ± 0.5 t km^{-2} yr^{-1}). During the mid-1990s, capelin accounted for 63% of matter consumed while the two other main prey groups were shrimp and planktivorous small pelagics (9% of matter consumed each). From the mid-1990s to early 2000s, there was an increase in the amount of matter consumed within the ecosystem (from 4.8 ± 0.5 to 7.3 ± 0.9 t km^{-2} yr^{-1}). The main prey was capelin (43% of matter consumed), followed by shrimp (22%) and planktivorous small pelagics (14%). More specifically, capelin, planktivorous small pelagics, female shrimp, and male shrimp were the main prey in the system during the early 2000s (Figure 5).

Main causes of shrimp mortality

Shrimp was consumed by twenty predators during each period. Predation dominated total mortality of shrimp (87% of total mortality) during the mid-1980s (Figure 6). Fishing and other mortality causes accounted for 6% each of total mortality. Redfish was the main predator, although the same diet was used in all three periods (this diet was obtained when the redfish biomass was small and the shrimp biomass was increasing; stomach content data available from 1993 to 1999). It is possible that the proportion of shrimp in the redfish diet was less in the 1980s, when biomass of redfish was much greater relative to the shrimp biomass. The two other main predators were small and large cod. Annual mortality rates for predation, fishing, and other mortality causes were estimated at 1.5, 0.1, and 0.1 yr^{-1}, respectively (total: 1.8 yr^{-1}).

From the mid-1980s to mid-1990s, there was a three-fold decrease in total mortality (from 1.5 ± 0.2 to 0.6 ± 0.1 t km^{-2} yr^{-1}; Figure 6). Predation mortality decreased from 1.3 ± 0.2 t km^{-2} yr^{-1} during the mid-1980s to 0.4 ± 0.1 t km^{-2} yr^{-1} during the mid-1990s while fishing increased from 0.09 ± 0.01 t km^{-2} yr^{-1} to 0.16 ± 0.02 t km^{-2} yr^{-1} during the same time period. Predation dominated total mortality (68% of total mortality), while fishing and other mortality causes accounted for 27 and 5%, respectively during the mid-1990s. Redfish, small cod, and Greenland halibut were the main predators of shrimp. Annual mortality rates for predation, fishing, and other mortality causes were estimated at 0.6, 0.3, and 0.0 yr^{-1}, respectively (total: 1.0 yr^{-1}).

From the mid-1990s to early 2000s, there was a three-fold increase in total mortality (from 0.6 ± 0.1 to 1.9 ± 0.2 t km^{-2} yr^{-1}; Figure 6). Fishing increased from 0.16 ± 0.02 t km^{-2} yr^{-1} during the mid-1990s to 0.24 ± 0.01 t km^{-2} yr^{-1} during the early 2000s. Also, predation mortality increased from 0.4 ± 0.1 t km^{-2} yr^{-1} during the mid-1990s to 1.6 ± 0.2 t km^{-2} yr^{-1} during the early 2000s. Predation dominated total mortality (82% of total mortality) while fishing and other mortality causes accounted for 12 and 5%, respectively, during the early 2000s. Small Greenland halibut was the main predator (29% of total mortality), followed by redfish (16%) and large cod (9%). Annual mortality rates for predation, fishing, and other mortality causes were estimated at 1.0, 0.2, and 0.1 yr^{-1}, respectively (total: 1.2 yr^{-1}).

For the early 2000s, redfish, small Greenland halibut, and small demersals were the main predators of female shrimp while male shrimp were mainly consumed by small Greenland halibut and large cod (Figure 7). Annual mortality rates for predation, fishing, and other mortality causes were estimated at 0.9, 0.2, and 0.1 yr^{-1} (total: 1.1 yr^{-1}) for females and 1.2, 0.1, and 0.1 yr^{-1} (total: 1.4 yr^{-1}) for males, respectively.

The trophic relationships between shrimp and their main predators should be relatively well estimated by the models. The changes in the proportion of shrimp ingested by cod, Greenland halibut, and redfish over the three time periods were constrained by samples from the northern Gulf whenever possible. Stomach content data were available for large and small cod for 1985–1987, 1994–1996, and 2000–2002 while stomach content data for small and large Greenland halibut were not available for the 1985–1987 period only. Also, the proportions of female and male shrimp in the diets of cod and Greenland halibut for the early 2000s were based on stomach contents, while the proportion of shrimp in the diet compositions of the other species was divided in two to account for the proportions of female and male shrimp.

Trophic links related to shrimp

Our results partly support the "top-down" view of species interactions (predators can suppress lower trophic levels) for the predator–prey relationship between cod and shrimp found by Worm and Myers (2003). Based on a meta-analysis of time-series data across nine regions in the North Atlantic, these authors calculated strong inverse correlations between shrimp and cod that they interpreted as "top-down" effects. In the northern Gulf of St. Lawrence, even though cod exerted a significant predation pressure on shrimp during the mid-1980s, redfish consumed as much shrimp as cod did (Figure 8). However, large cod were also the main predators of both small cod and redfish. The strong inverse correlations between shrimp and cod could result from both direct (as predators) and indirect (as the main predators of intermediate predators, e.g., small cod and redfish) predation by large cod. Moreover, the simultaneous decline of cod and redfish stocks in the early 1990s could have exacerbated the negative relationship between cod and shrimp observed by Worm and Myers (2003).

During the mid-1990s, with the decreases in cod and redfish biomass, the total predation on shrimp decreased. Although the predation by Greenland halibut stayed at about the same level between the two periods, the species became the main predator of shrimp (Figure 8). The fishing mortality increased by a factor of nearly two from the mid-1980s to the mid-1990s in accordance with the increase in commercial landings.

During the early 2000s, the total predation impact on shrimp increased due to a higher contribution of most predators (Figure 8). However, small Greenland halibut was the main cause of mortality on shrimp, with a 9-fold increase between the mid-1990s and the early 2000s. Small and large Greenland halibut progressively replaced small and large cod and redfish as the main predators of shrimp. The fishing mortality also increased by nearly 100%.

DISCUSSION / CONCLUSION

The net decrease in biomass of the demersal species and the ensuing drop in predation from the mid-1980s to the mid-1990s led to an ecosystem structure dominated by small-bodied pelagic species and marine mammals in the northern Gulf of St. Lawrence. This has left only marine mammals as top predators during the mid-1990s, and marine mammals and small Greenland halibut during the early 2000s (Savenkoff et al. submitted).

During the early 2000s, small Greenland halibut had the highest biomass for fish species (1.31 ± 0.30 t km^{-2}) and were not heavily consumed (predation mortality: 29% of total mortality) in the ecosystem. In the models, we supposed that they were not recruited to the fishery. It is likely that their effect on the ecosystem, especially on shrimp, will increase in the future. Indeed, small Greenland halibut mainly consumed capelin, shrimp, and large zooplankton (34%, 34%, and 26% of the diet composition, respectively) (Figure 9). From the mid-1980s to early 2000s, the proportion of fish prey in the diet composition of small Greenland halibut decreased from 67% to 40% while the proportions of shrimp and large zooplankton increased accordingly. Shrimp were also among the most important prey of large Greenland halibut (Figure 10). The proportion of fish prey in the diet composition of large Greenland halibut also decreased from 74% during the mid-1980s to 55% during the early 2000s, with a reciprocal increase in the proportion of shrimp.

Declines in groundfish stocks were often accompanied by increases in the abundances of benthic crustaceans such as northern shrimp and snow crabs. Various hypotheses have been proposed to explain the increase in abundance of benthic prey species, including changes in ocean temperature (which might affect cod and crustaceans differently), release from cod predation (and possibly predation by other large demersal fishes), or both (Anderson 2000, Berenboim et al. 2000, Koeller 2000, Lilly et al. 2000, Worm and Myers 2003). In the northern Gulf, shrimp biomass almost doubled from the mid-1980s to the early 2000s. Thus, shrimp showed an increase in biomass in the northern Gulf ecosystem concurrent with the net decrease in biomass of large piscivorous predators. In the northern Gulf, there was a net decrease in total mortality and predation on shrimp from the mid-1980s to mid-1990s while fishing mortality increased over the same time period. From the mid-1990s to early 2000s, total mortality, predation, and fishing mortality all increased. However, predation remained the main cause of shrimp mortality in the northern Gulf for each time period. Greenland halibut progressively replaced cod and redfish as the main predators of shrimp all over the three periods.

The biomass of Greenland halibut sharply increased starting in 1995 (from 22,000 t in 1995 to near 80,000 t in 2001). Commercial catches of large Greenland halibut increased in the 1980s to reach an all-time high in 1987 (11,000 t) but declined at the beginning of the 1990s and are now around 3,000 t (Morin and Bernier 2003). The Gulf of St. Lawrence population of Greenland halibut is considered to be a small stock, isolated from the main Northwest Atlantic stock, completing its entire life cycle within the Gulf (Morin and Bernier 2003). This deep-water flatfish is found at depths of 130–500 m, and so predation by Greenland halibut on shrimp may occur over a large part of the year due to the overlapping distributions of Greenland halibut and shrimp observed in summer and fall.

Until now, the relative effects and interplay of fishing and predation on shrimp have been poorly investigated in the northern Gulf of St. Lawrence. Nevertheless, spatial and temporal variations in the dynamics of shrimp populations will, inevitably, influence landings and harvesting strategies. The fishery is managed by total allowable catches (TACs). To improve management practices, the exploitation rate or the harvesting rules should be adjusted taking into account the condition of the population (e.g., different conditions due to variations in mortality from predation and fishing, in reproductive parameters, and in recruitment success). Ecosystem models could become powerful new tools for fishery management. Results from these models already provide valuable information on the impact of fishing relative to the effects of predation and natural mortality other than predation on the fish and invertebrate communities.

Modelling of large marine ecosystems is still in its infancy. Our current models, even with 30 compartments, still represent simplifications of the trophic interactions in the northern Gulf of St. Lawrence. The validity of any conclusion regarding the ecosystem being studied depends on the input data (and the confidence that we have in them). This work is the result of a huge effort to assemble data on the biological characteristics of species occurring in the northern Gulf of St. Lawrence at three time periods. Even though most of the data are good estimates for the 4RS ecosystem, some input values are rough estimates only, meaning that these values are assembled from different literature sources and not from independently measured parameters. Some errors in parameter estimates could significantly alter the system's biomass budget, especially for the most important species of the ecosystem, or produce a totally different balanced solution. Overall, even though the model is not a perfect representation of reality, it is probably as good as it can be with the information available. This illustrates the need for further work to improve the input parameters in order to enhance the quality of future modelling efforts. Recurrent

information on the impact of fishing and predation on shrimp in the Gulf of St. Lawrence has to be collected to adapt management strategies to the current predator and prey stock situation and to ensure that the biomass of one of the most important forage species remains at a level that meets the predator needs in the future.

ACKNOWLEDGMENTS

We are grateful to Simon-Pierre Despatie, Hugo Bourdages, Red Méthot, and colleagues who made data available for this report. Gratitude is extended to Laure Devine for reading and commenting on the manuscript. We also thank Martin Castonguay (Institut Maurice-Lamontagne, Mont-Joli, Québec) and David Orr (Northwest Atlantic Fisheries Centre, St. John's, Newfoundland) for their comments and reviews of the manuscript.

See the CDEENA web site at http://www.osl.gc.ca/cdeena/en/accueil.shtml.

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Table 1. Functional groups used in modelling in the northern Gulf of St. Lawrence for each time period.

Group name	Main species
Cetaceans[a]	Mysticeti or baleen whales: *Balaenoptera physalus*, *Balaenoptera acutorostrata*, *Megaptera novaeangliae* Odontoceti or toothed whales: *Lagenorhynchus acutus*, *L. albirostris*, *Phocoena phocoena*
Harp seals[b]	*Pagophilus groenlandicus*
Hooded seals[b]	*Cystophora cristata*
Grey seals[c]	*Halichoerus grypus*
Harbour seals[c]	*Phoca vitulina*
Seabirds	*Phalacrocorax carbo*, *P. auritus*, *Larus delawarensis*, *L. argentatus*, *L. marinus*, *Sterna hirundo*, *S. paradisaea*, *Cepphus grylle*, *Oceanodroma leucorhoa*, *Morus bassanus*, *Rissa tridactyla*, *Uria aalge*, *Alca torda*, *Fratercula arctica*
Large Atlantic cod (> 35 cm)	*Gadus morhua*
Small Atlantic cod (≤ 35 cm)	*Gadus morhua*
Large Greenland halibut (> 40 cm)	*Reinhardtius hippoglossoides*
Small Greenland halibut (≤ 40 cm)	*Reinhardtius hippoglossoides*
American plaice	*Hippoglossoides platessoides*
Flounders	*Limanda ferruginea*, *Glyptocephalus cynoglossus*, *Pseudopleuronectes americanus*
Skates	*Amblyraja radiata*, *Malacoraja senta*, *Leucoraja ocellata*
Redfish	*Sebastes mentella*, *Sebastes fasciatus*
Large demersal feeders	*Urophycis tenuis*, *Melanogrammus aeglefinus*, *Centroscyllium fabricii*, *Anarhichas* spp., *Cyclopterus lumpus*, *Lycodes* spp., Macrouridae, Zoarcidae, *Lophius americanus*, *Hippoglossus hippoglossus*
Small demersal feeders	*Myoxocephalus* spp., *Tautogolabrus adspersus*, *Macrozoarces americanus*, juvenile large demersals
Capelin	*Mallotus villosus*
Sand lance[d]	*Ammodytes* spp.
Arctic cod[e]	*Boreogadus saida*

Table 1. Cont.

Group name	Main species
Large pelagic feeders	*Squalus acanthias*, *Pollachius virens*, *Merluccius bilinearis*
Piscivorous small pelagic feeders	*Scomber scombrus*, piscivorous myctophids and other mesopelagics, *Illex illecebrosus*, piscivorous juvenile large pelagics
Planktivorous small pelagic feeders	*Clupea harengus*, planktivorous myctophids and other mesopelagics, *Scomberesox saurus*, *Gonatus* spp., planktivorous juvenile large pelagics
Shrimp[f]	*Pandalus borealis*, *P. montagui*, *Argis dentata*, *Pasiphaea multidentata*
Crabs[g]	*Chionoecetes opilio*, other non-commercial species (e.g., *Hyas* spp.)
Echinoderms	*Echinarachnius parma*, *Strongylocentrotus pallidus*, *Ophiura robusta*
Molluscs	*Mesodesma deauratum*, *Cyrtodaria siliqua*
Polychaetes	*Exogone hebes*
Other benthic invertebrates	Miscellaneous crustaceans, nematodes, other meiofauna
Large zooplankton (> 5 mm)	Euphausiids, chaetognaths, hyperiid amphipods, cnidarians and ctenophores (jellyfish), mysids, tunicates >5 mm, ichthyoplankton
Small zooplankton (< 5 mm)	Copepods (mainly *Calanus finmarchicus*, *C. hyperboreus*, and *Oithona similis*), tunicates < 5 mm, meroplankton, heterotrophic protozoa (flagellates, dinoflagellates, and ciliates)

Table 1. Cont.

Group name	Main species
Phytoplankton	Diatom species such as *Chaetoceros affinis*, *C.* spp., *Leptocylindrus minimus*, *Thalassiosira nordenskioeldii*, *T.* spp., *Fragilariopsis* spp., and a mixture of autotrophic and mixotrophic organisms including Cryptophytes, dinoflagellates, Prasinophytes, and Prymnesiophytes
Detritus	Sinking particulate organic matter including both large particles (consisting of animal carcasses and debris of terrigenous and coastal plants) and fine particles (mostly from planktonic organisms, including feces, moults, phytoplankton aggregates, and bacteria)

[a]: Cetaceans were separated into two groups for the early 2000s: the mysticeti (baleen whales) and the odontoceti (toothed whales).
[b]: Harp and hooded seals were grouped in the early 2000s.
[c]: Grey and harbour seals were grouped in the early 2000s.
[d]: Included in the planktivorous small pelagic feeders in the early 2000s.
[e]: Included in the capelin group in the early 2000s.
[f] Shrimp were separated into large shrimp, mainly females ($\geq$ 22 mm CL; mainly *Pandalus borealis*), and small shrimp ($<$ 22 mm CL) in the early 2000s.
[g]: Crabs were separated into small ($\leq$ 45 mm CW) and large ($>$ 45 mm CW) crabs in the early 2000s.

Table 2. Observed biomass, lower and upper modelling constraints, and estimated fluxes for shrimp made using inverse modelling for each ecosystem and each time period.

Parameter	1985–1987	1994–1996	2000–2002	
	All	All	Females > 22 mm	Males < 22 mm
Observed mean biomass (t km^{-2})	0.83	0.62	0.95	0.62
Observed minimum biomass (t km^{-2})	0.58	0.38	0.72	0.48
Observed maximum biomass (t km^{-2})	1.08	0.84	1.12	0.72
Observed mean production (t km^{-2} yr^{-1})	0.87	0.64	0.96	0.63
Constrained minimum production (t km^{-2} yr^{-1})	0.37	0.24	0.46	0.30
Constrained maximum production (t km^{-2} yr^{-1})	1.57	1.22	1.63	1.04
Estimated production (t km^{-2} yr^{-1})	1.47	0.59	1.04	0.89
Observed mean consumption (t km^{-2} yr^{-1})	5.79	4.27	6.41	4.17
Constrained minimum consumption (t km^{-2} yr^{-1})	2.89	2.13	3.20	2.08
Constrained maximum consumption (t km^{-2} yr^{-1})	8.68	6.40	9.61	6.25
Estimated consumption (t km^{-2} yr^{-1})	6.67	2.63	5.97	4.50
Observed mean catch (t km^{-2} yr^{-1})	0.09	0.15	0.14	0.09
Constrained minimum catch (t km^{-2} yr^{-1})	0.08	0.14	0.12	0.08
Constrained maximum catch (t km^{-2} yr^{-1})	0.11	0.17	0.16	0.11
Estimated catch (t km^{-2} yr^{-1})	0.09	0.16	0.15	0.09

Table 3. Diet composition of shrimp used in modelling of the northern Gulf for 1985–1987 and 1994–1996. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

				1985–1987	1994–1996
Group	Mean ± SD[a]	Min	Max	Est	Est
Shrimp	**0.0**	0.0	0.0	0.0	0.0
Polychaetes	1.5	**0.8**	**2.3**	1.5	2.2
Other bent. inver.	1.5	**0.8**	**2.3**	1.8	2.2
Large zooplankton	12.0	**6.0**	**18.0**	9.1	18.0
Small zooplankton	24.0	**12.0**	**36.0**	24.1	28.3
Phytoplankton	8.5	**4.3**	**12.8**	9.7	12.8
Detritus	52.5	**26.3**	**78.8**	53.8	36.4
Total	100.0	50.0	150.0	100.0	100.0
TRN	7				

[a]: No variance (available only as point estimates): Min = mean – (mean x 50%), Max = mean + (mean x 50%).

Table 4. Diet composition of female and male shrimp used in modelling of the northern Gulf for 2000–2002. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

					Females	Males
Group	Mean	± SD[a]	Min	Max	Est	Est
Female shrimp	**0.0**	0.0	0.0	0.0	0.0	0.0
Male shrimp	**0.0**	0.0	0.0	0.0	0.0	0.0
Polychaetes	1.5	1.9	**0.0**	**3.4**	3.4	3.1
Other bent. inver.	1.5	2.2	**0.0**	**3.7**	2.2	2.6
Large zooplankton	12.0	15.0	**0.0**	**27.0**	13.1	16.1
Small zooplankton	24.0	30.3	**0.0**	**54.3**	38.1	39.1
Phytoplankton	8.5	7.0	**1.5**	**15.5**	14.1	14.2
Detritus	52.5	43.5	**9.0**	**96.0**	29.1	24.8
Total	100.0		10.4	199.9	100.0	100.0
TRN	8					

[a]: All the proportions of prey in the diet composition were available only as point estimates. SD was then calculated as $DC^{obs}_{x \to y}$ *CV($DC^{obs}_{x \to u}$)mean (SD = CV*Mean), with $DC^{obs}_{x \to y}$ representing the proportion of prey x consumed by female or male shrimp and CV($DC^{obs}_{x \to u}$)mean representing the average of all coefficients of variation of the proportion of prey x consumed by the other groups u of the modelled ecosystem. Min = mean – SD, Max = mean + SD.

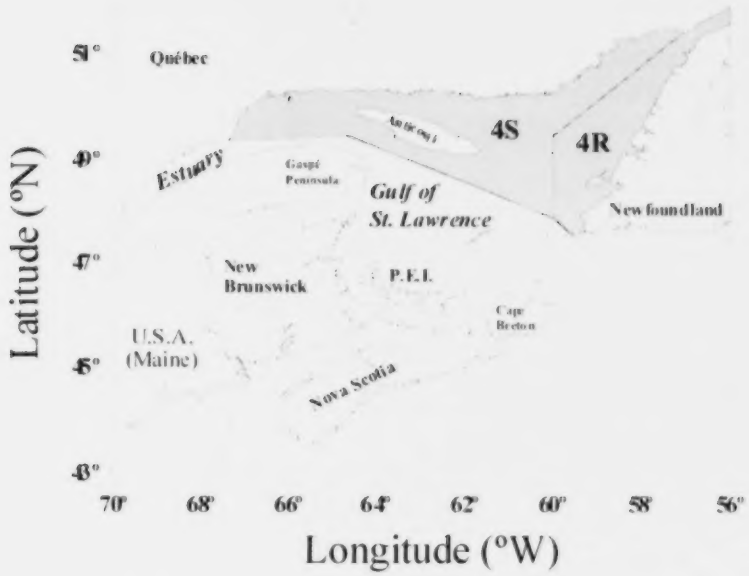

Figure 1. Northern Gulf of St. Lawrence (NAFO divisions 4RS) equivalent to a total area of 103,812 km^2.

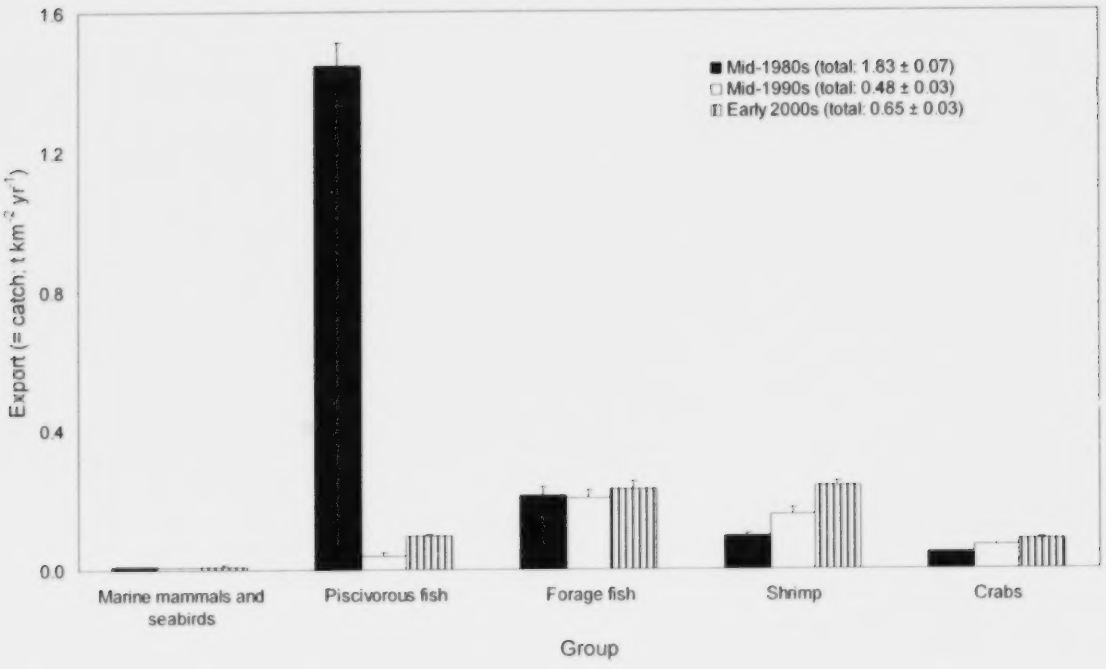

Figure 2. Distribution of catches by trophic groups for each time period estimated by the models. Bars show mean values and SD.

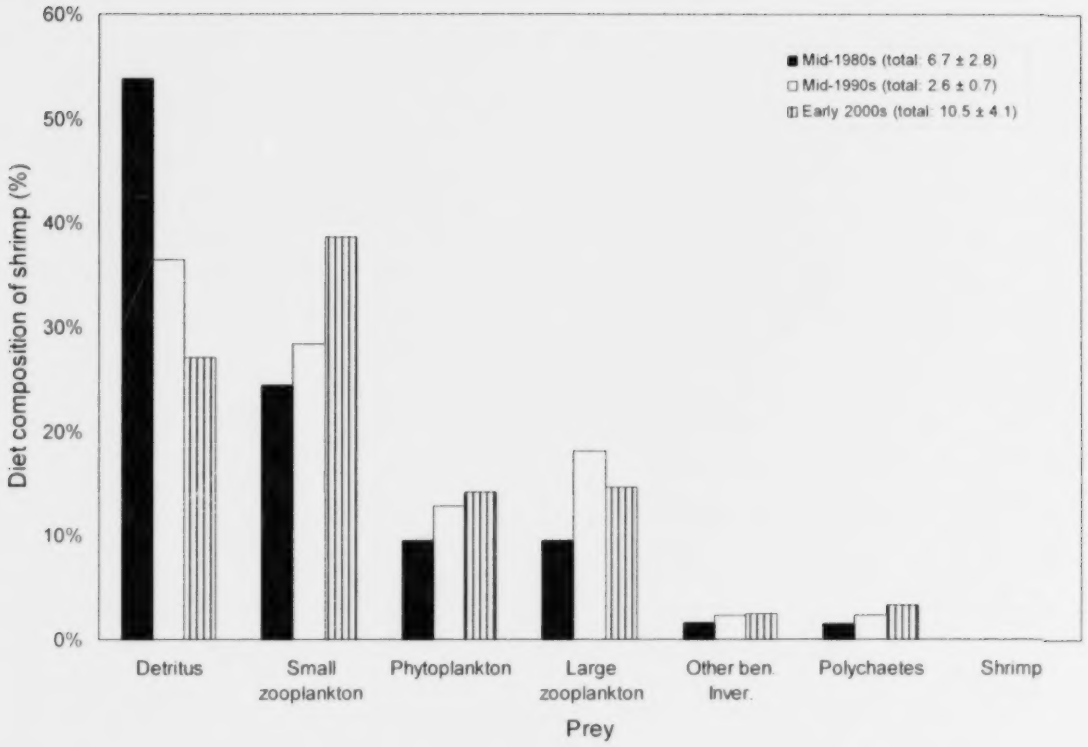

Figure 3. Diet composition of shrimp estimated for each time period. Total shrimp consumption for each time period (in t km^{-2} yr^{-1}) is shown in the legend.

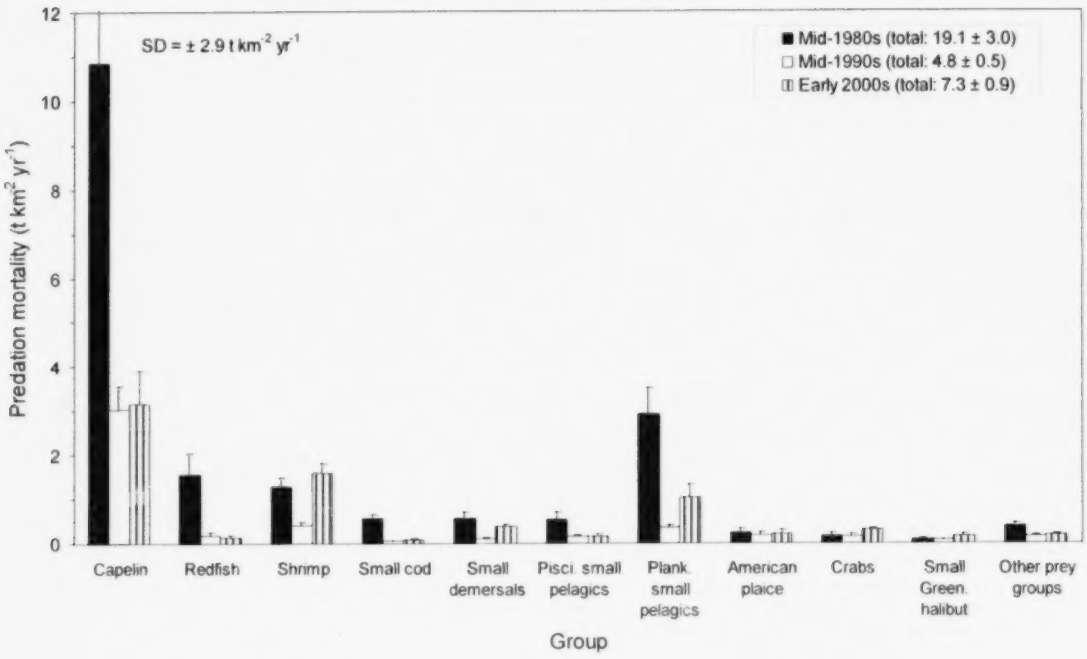

Figure 4. Main vertebrate and crustacean prey consumed in the northern Gulf of St. Lawrence for each time period. The other prey groups accounted for 2% (flounders: 0.8%, large demersals: 0.6%, and other species: < 0.3% each) during the mid-1980s, 3% (large cod: 1.0%, large demersals and skates: 0.7% each, and other species: < 0.4% each) during the mid-1990s, and 2% (large cod: 0.9%, large demersals: 0.6%, and other species: < 0.3% each) during the early 2000s. SD is shown.

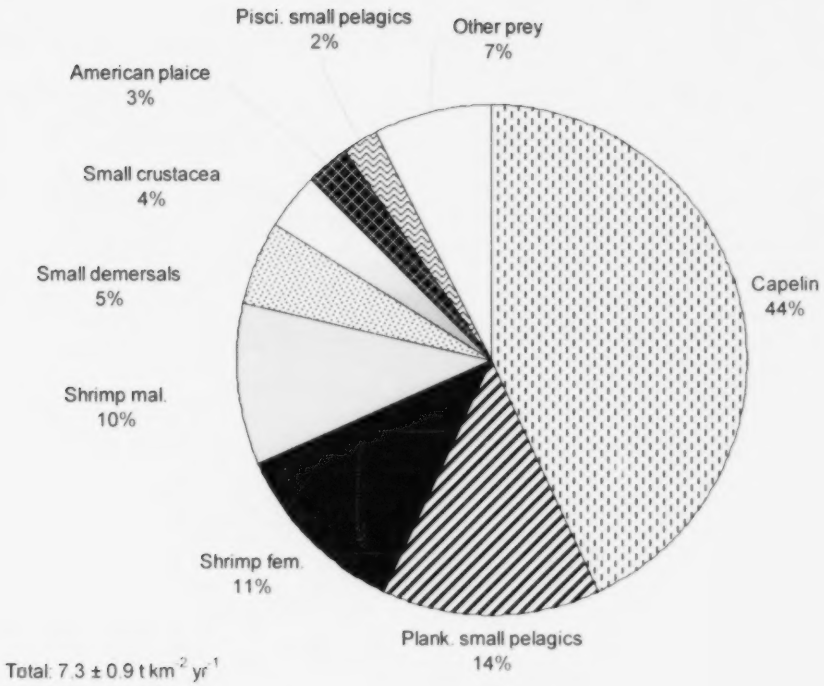

Figure 5. Main vertebrate and crustacean prey consumed in the northern Gulf estimated for the early 2000s.

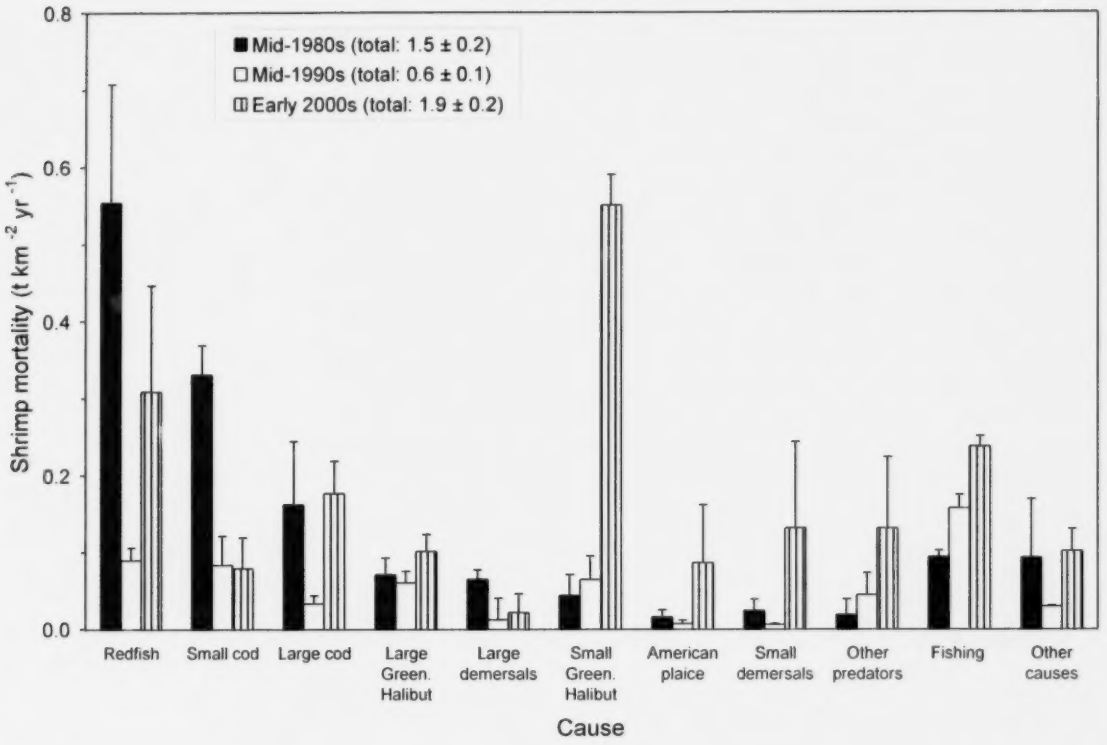

Figure 6. Main mortality causes (fishing, predation, and natural mortality other than predation; i.e., other mortality causes) on shrimp estimated for each time period. Bars show mean values and SD.

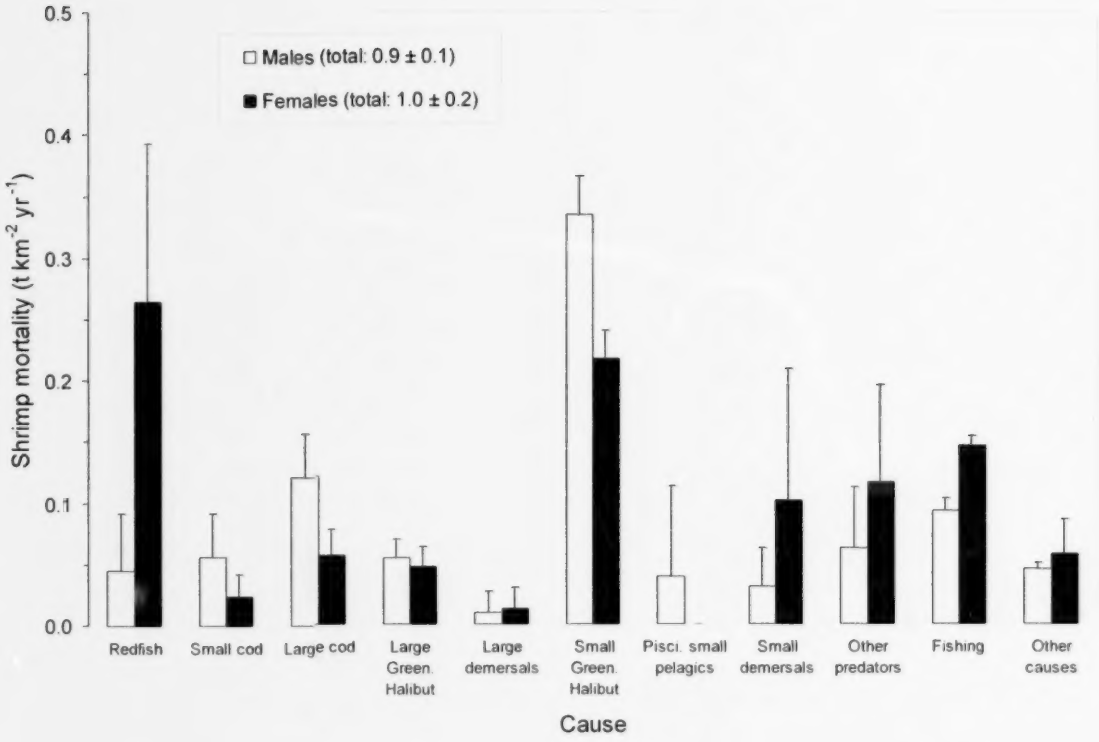

Figure 7. Main mortality causes (fishing, predation, and natural mortality other than predation; i.e., other mortality causes) on male and female shrimp estimated for the early 2000s. Bars show mean values and SD.

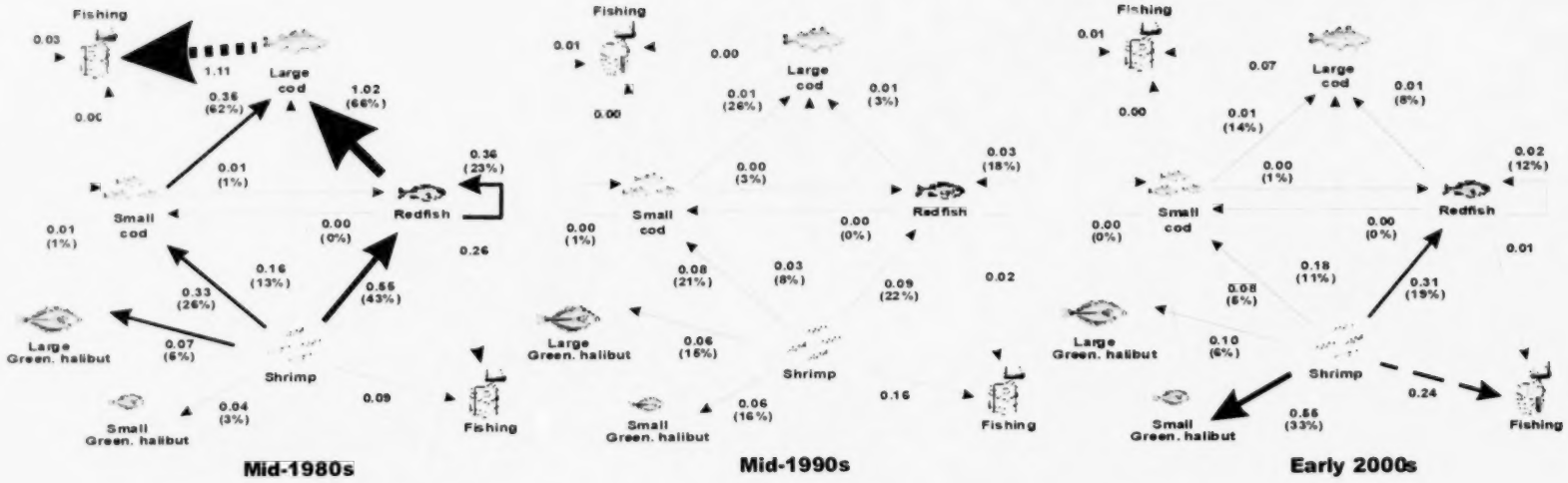

Figure 8. Main predation fluxes (t km^{-2} yr^{-1}) on shrimp for each time period. The contribution (%) of each predation flux to total predation mortality is also shown in parentheses. For comparisons, fishing mortality fluxes (t km^{-2} yr^{-1}) are also included.

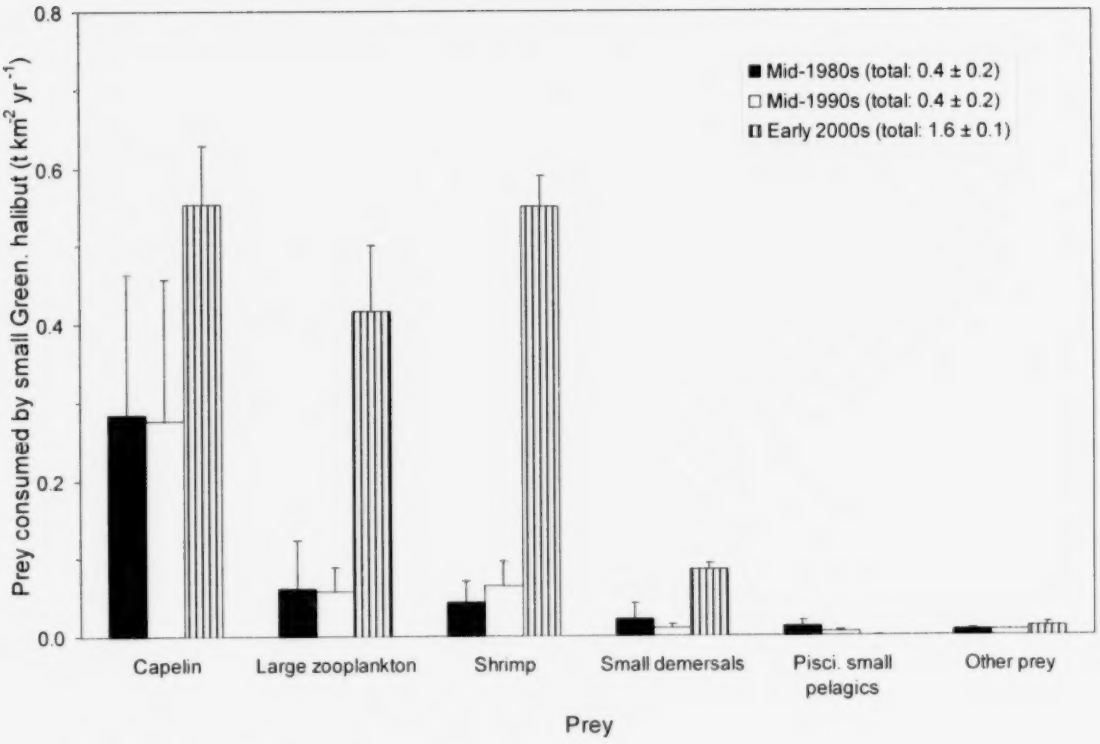

Figure 9. Predation by small Greenland halibut (< 40 cm) estimated for each time period. Total consumption for small Greenland halibut per period (in t km^{-2} yr^{-1}) is shown in the legend. Bars show mean values and SD.

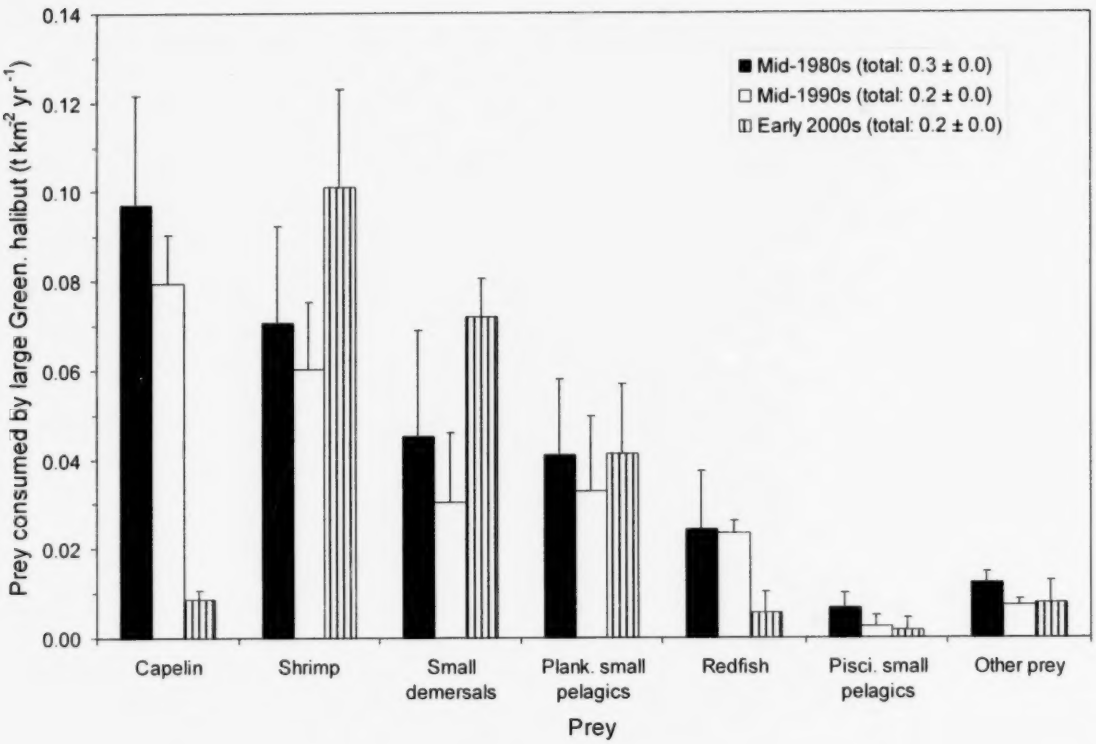

Figure 10. Predation by large Greenland halibut (> 40 cm) estimated for each time period. Total consumption for large Greenland halibut per period (in t km^{-2} yr^{-1}) is shown in the legend. Bars show mean values and SD.